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Response of soil respiration to short-term changes in precipitation and nitrogen addition in a desert steppe

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Abstract: Changes in precipitation and nitrogen (N) addition may significantly affect the processes of soil carbon (C) cycle in terrestrial ecosystems, such as soil respiration. However, relatively few studies have investigated the effects of changes in precipitation and N addition on soil respiration in the upper soil layer in desert steppes. In this study, we conducted a control experiment that involved a field simulation from July 2020 to December 2021 in a desert steppe in Yanchi County, China. Specifically, we measured soil parameters including soil temperature, soil moisture, total nitrogen (TN), soil organic carbon (SOC), soil microbial biomass carbon (SMBC), soil microbial biomass nitrogen (SMBN), and contents of soil microorganisms including bacteria, fungi, actinomyces, and protozoa, and determined the components of soil respiration including soil respiration with litter (R_{S+L}), soil respiration without litter (R_S), and litter respiration (R_L) under short-term changes in precipitation (control, increased precipitation by 30%, and decreased precipitation by 30%) and N addition (0.0 and 10.0 g/(m^2·a)) treatments. Our results indicated that short-term changes in precipitation and N addition had substantial positive effects on the contents of TN, SOC, and SMBC, as well as the contents of soil actinomyces and protozoa. In addition, N addition significantly enhanced the rates of R_{S+L} and R_S by 4.8% and 8.0% ($P<0.05$), respectively. The increase in precipitation markedly increased the rates of R_{S+L} and R_S by 2.3% ($P<0.05$) and 5.7% ($P<0.001$), respectively. The decrease in precipitation significantly increased the rates of R_{S+L} and R_S by 12.9% ($P<0.05$) and 23.4% ($P<0.001$), respectively. In contrast, short-term changes in precipitation and N addition had no significant effects on R_L rate ($P>0.05$). The mean R_L/R_{S+L} value observed under all treatments was 27.63%, which suggested that R_L is an important component of soil respiration in the desert steppe ecosystems. The results also showed that short-term changes in precipitation and N addition had significant interactive effects on the rates of R_{S+L}, R_S, and R_L ($P<0.001$). In addition, soil temperature was the most important abiotic factor that affected the rates of R_{S+L}, R_S, and R_L. Results of the correlation analysis demonstrated that the rates of R_{S+L}, R_S, and R_L were closely related to soil temperature, soil moisture, TN, SOC, and the contents of soil microorganisms, and the structural equation model revealed that SOC and SMBC are the key factors influencing the rates of R_{S+L}, R_S, and R_L. This study provides further insights into the characteristics of soil C emissions in desert steppe ecosystems in the context of climate change, which can be used as a reference for future related studies.

Keywords: soil respiration; litter respiration; nitrogen deposition; soil carbon; soil microorganisms; climate change; desert steppe ecosystems

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1 Introduction

Soil respiration is the primary process that controls carbon (C) emissions from the soil to the atmosphere and plays an important role in adjusting the response of the C cycle in terrestrial ecosystems to natural and human-induced disturbances (Yu et al., 2020; Qin et al., 2023; Wang et al., 2023). Hanson et al. (2000) showed that plant roots, soil microorganisms, and litter respiration (R_L) are the primary components of soil respiration. Soil respiration is the second largest process of C flux in terrestrial ecosystems and accounts for approximately 68–98 Pg C every year (Bond-Lamberty and Thomson, 2010). In addition, soil respiration is considered to be a sensitive indicator of the metabolic activity of soil microorganisms, the process of litter decomposition, and the conversion of soil C to atmospheric C (Harper et al., 2005; Borken et al., 2006; Zhou et al., 2014). However, soil respiration is highly vulnerable to global climate change, including nitrogen (N) deposition and changes in temperature and precipitation (Shi et al., 2019; Song et al., 2020; Xiao et al., 2020). Therefore, studying the dynamics of soil respiration and its influencing factors will help to understand the relationship between the dynamics of soil C emissions and climate change.

As one of the major factors of global climate change, atmospheric N deposition has a substantial impact on the structure and function of ecosystems, such as the C cycle in grassland ecosystems (Chen et al., 2020; Yang et al., 2022a; Yang et al., 2022c). Indeed, several previous studies have reported that N deposition affects soil respiration by altering plant growth and development, litter decomposition, and soil microenvironments (Peng et al., 2011; Zhang et al., 2019a). In addition, other studies have revealed inconsistent results, demonstrating that N addition facilitates (Song et al., 2011; Wang et al., 2019a), inhibits (Phillips and Fahey, 2007; Mo et al., 2008; Yan et al., 2010), or does not affect soil respiration (Qi et al., 2014; Zhu et al., 2015). However, this inconsistency in results may be owing to the patterns of C fixation induced by N and the differences in the metabolic activity of soil microorganisms among different ecosystems (Lee and Jose, 2003). Wang et al. (2019a) highlighted how the positive impact of N addition increased the input of aboveground litter, which may promote the utilization of belowground C and soil respiration, particularly in desert steppes. Therefore, it is important to investigate the effects of N addition on soil respiration to accurately predict the characteristics of C emissions from desert steppes in the context of increased global N deposition.

As a key factor that drives ecological processes, changes in precipitation can substantially affect the C cycle in terrestrial ecosystems, as well as the source and sink functions of terrestrial ecosystems, particularly in desert steppe areas (Zhang et al., 2019b; Legesse et al., 2022; Zhang et al., 2022a). Zhang et al. (2019d) demonstrated the substantial effects of changes in precipitation in promoting soil respiration in arid ecosystems. Indeed, those effects are enhanced by several ecological processes (Talmon et al., 2011; Liu et al., 2016), such as plant growth (Zhou et al., 2016), soil microorganisms (Ren et al., 2018), soil enzyme activity (Zhao et al., 2016), and the sensitivity of the rates of soil respiration to temperature (Suseela et al., 2012). However, some studies have reported that changes in precipitation can inhibit soil respiration (Harper et al., 2005; Liu et al., 2018), which may be related to the availability of different substrates and the activity of extracellular enzymes that degrade C (Knapp et al., 2002; Ren et al., 2017). Therefore, it is necessary to study the responses of soil respiration to changes in precipitation in desert steppe ecosystems in more detail.

Litter plays an important role in the C cycle of grassland ecosystems (Schlesinger and Andrews, 2000; Zhang et al., 2012). Wang et al. (2009a) demonstrated that litter is one of the sources of soil C pool in desert steppe ecosystems. Indeed, litter provides nutrients for soil microorganisms, improves the composition of microbial communities, and enhances microbial respiration (Zhao et al., 2020; Craig et al., 2022). Moreover, litter can alter the soil

microenvironments, change the efficiency of soil nutrient use, and affect soil respiration (Sun et al., 2019; Connell et al., 2022). Niu et al. (2019) demonstrated that the removal or addition of litter to soils could alter soil organic C (SOC) content, thereby significantly reducing or increasing soil respiration. The contribution of litter to soil respiration is one of the most important indicators of the role of litter in the soil C cycle (Huang et al., 2017) and reflects the mechanism of allocating C to the aboveground and belowground plant parts to some extent (Wang et al., 2009b). Therefore, it is important to comprehensively investigate the contribution of litter to soil respiration to reveal the role of litter in the cycling of materials and in the processes of energy flow between plants and soil.

The desert steppe is a typical ecosystem that is vulnerable to environmental changes, such as changes in precipitation and N addition (Olive et al., 2019; Wang et al., 2019b; Zhang et al., 2022b). However, the responses of soil respiration with litter (R_{S+L}) to changes in precipitation and N addition in desert steppes remain unclear (Zhang et al., 2020; Zhang et al., 2022c). In addition, most observational studies on soil respiration in desert steppes primarily focused on the effects of plant community and nutrient addition on soil respiration (Zhang et al., 2015). To date, few studies have monitored soil respiration and investigated the effects of litter on soil respiration (Han et al., 2007; Wen et al., 2020). The characteristics of C dioxide (CO_2) emissions derived from litter in the upper soil layer in a desert steppe in China were analyzed to provide basic information to estimate the C balance and study the primary mechanisms that control the C cycle in desert steppe ecosystems, therefore accelerating the improvement and restoration processes of desert steppes (Wang et al., 2019a). In this study, we investigated the impacts of short-term changes in precipitation, N addition, and their interaction on R_{S+L}, soil respiration without litter (R_S), and R_L, as well as the effects of biotic (soil microorganisms) and abiotic (soil physical-chemical properties) factors on soil respiration (R_{S+L}, R_S, and R_L) under different treatments in a desert steppe in Yanchi County, China. We hypothesized that: (1) an increase in precipitation and N addition can accelerate soil respiration, due to the increased soil nutrients and enhanced soil microbial activity, while a decrease in precipitation may restrain soil respiration; and (2) the rates of soil respiration are strongly associated with soil temperature, moisture, and microbial community. Our research will help to understand the dynamics of soil respiration in desert steppes and provide a scientific basis to study the C cycle in desert steppe ecosystems.

2 Materials and methods

2.1 Study area

The study area (37°04′–38°10′N, 106°30′–107°47′E; 1600 m a.s.l.) is located in Yanchi County in the eastern part of Ningxia Hui Autonomous Region, China. This county is an important agro-pastoral transition zone that consists of vast dry grasslands and desert steppes from southeast to northwest. The study area is characterized by a mid-temperate continental monsoon climate, which has semi-arid to arid transition zones. The annual average temperature and average annual precipitation are 8.4°C and 280 mm, respectively. Gray calcium soil is the dominant soil type in the study area (Spaargaren and Deckers, 1998), and the vegetation types are primarily composed of shrub, sandy vegetation, and desert vegetation. The dominant plant species in the fields that do not produce litter include *Pennisetum centrasiaticum*, *Astragalus melilotoides*, *Cleistogenes squarrosa*, *Setaria viridis*, *Gueldenstaedtia verna*, *Lespedeza potaninii*, *Euphorbia esula*, *Oxytropis racemose*, *Bassia dasyphylla*, *Eragrostis Pilosa*, and *Polygala tenuifolia*; in addition, the dominant species that produce litter contain *Artemisia scoparia*, *Sophora alopecuroides*, *Stipa breviflora*, and *Agropyron mongolicum* (Table S1).

2.2 Experimental design

In this study, experiments were conducted from July 2020 to December 2021 using a randomized complete block design with six treatment plots (2 m×6 m for each) for total and three replicates for each treatment plot. In this experiment, we considered three precipitation levels, namely the

control (CK), increased precipitation by 30% (IP), and decreased precipitation by 30% (DP), as well as two N addition rate levels, namely 0.0 g/(m^2·a) (N_0) and 10.0 g/(m^2·a) (N_{10}) (Bai et al., 2010). It should be noted that we utilized self-made V-shaped gutters made of transparent plexiglass to ensure the amount of the decreased precipitation in the corresponding treatment plots. In addition, the increased precipitation in the treatment plots was achieved by collecting rainwater from the gutters after precipitation events using buckets and then spraying it evenly onto the treatment plots with a watering can. N was applied in the form of urea (CH_4N_2O) at a rate of 2.5 g/m^2 in September 2020, March 2021, June 2021, and September 2021. The urea was first dissolved in clear water. The treatment without N addition was sprayed the same amount of water as the treatment with N addition. Hence, all treatments are as follows: CK+N_0, IP+N_0, DP+N_0, CK+N_{10}, IP+N_{10}, and DP+N_{10}. We installed polyvinyl chloride (PVC) boards buried 30 cm deep in the soil around each treatment plot to prevent the exchange of water and nutrients. In total, six PVC collars of respiratory rings (10 cm in height and 20 cm in diameter) were installed in each treatment plot. We irregularly removed living plants from each treatment plot. In one half of each treatment plot (1 m×6 m), 3 respiratory rings with litter were arranged to measure R_{S+L}, and in another half (1 m×6 m), 3 respiratory rings without litter were arranged to measure R_S.

2.3 Methods of measurement

Soil respiration was measured using an Li-8100 Automated Soil CO_2 Flux System (Li-COR Inc., Lincoln, NE, USA). Soil temperature and moisture in the 0–5 cm soil layer were measured simultaneously using a portable 8100-201 soil temperature probe (Li-COR Inc., Lincoln, NE, USA) and an 8100-204 soil moisture probe (Li-COR Inc., Lincoln, NE, USA), respectively. Soil respiration was measured on sunny days on 15–18 April, 19–22 July, 12–15 October, and 17–20 December in 2021. The measurement time was set from 12:00 to 10:00 of the next day (LST) at 2 h intervals, and the mean values on the three sunny days in April, July, October, and December were calculated and taken as the values corresponded to spring, summer, autumn, and winter, respectively (Yang et al., 2020). Owing to the low temperature at night in winter, the Li-8100 Automated Soil CO_2 Flux System could not normally determine soil respiration at 00:00–04:00, so the measurement values at 00:00, 02:00, and 04:00 were not included in winter. R_L in this study was estimated by calculating the differences between R_{S+L} and R_S, and litter respiration contribution (R_L/R_{S+L}) represented the contribution of litter respiration to the total soil respiration.

In addition, three replicates of soil samples (at depths of 0–5 cm) were randomly collected from half of each treatment plot (1 m×6 m) in July 2021. The collected soil samples were first passed through a 2-mm sieve and then stored in the laboratory at –4°C until further analysis. SOC was analyzed using the H_2SO_4–$K_2Cr_2O_7$ oxidation method followed by titration with $FeSO_4$ (Liu et al., 2017). The content of total nitrogen (TN) was determined using the micro Kjeldahl digestion procedure (Kjeltec 8400, FOSS, Koebenhavn, Denmark) (Liu et al., 2017). Soil microbial biomass carbon (SMBC) and soil microbial biomass nitrogen (SMBN) were analyzed using the chloroform fumigation extraction method, and the extract efficiency factors were 0.38 and 0.54, respectively (Guckert et al., 1986). Soil microbial communities (bacteria, fungi, actinomycetes, and protozoa) were determined using the phospholipid fatty acid method (Frostegrd et al., 1991), combined with the approach described by Bligh and Dyer (1959). The sum of the contents of phospholipid fatty acids 12:0, 13:0, 14:0, 15:0, 16:0, 22:0, and 24:0 indicated bacteria (Zelles, 1997); the sum of the contents of phospholipid fatty acids 18:1ω9c, 21:0, 23:0, and 18:2w6c indicated fungi (Ngosong et al., 2012); the sum of the contents of phospholipid fatty acids 10Me 17:0, 10Me 18:1ω7c, 10Me 19:1ω7c 10Me 17:1ω7c, and 10Me 18:0 indicated actinomycetes (Lechevalier, 1977); and the sum of the contents of phospholipid fatty acids 20:4ω6c, 20:3ω6c, 20:5ω3c, 19:3ω6c indicated protozoa (Massaccesi et al., 2015).

2.4 Statistical analysis

A linear model (Eq. 1) and an exponential model (Eq. 2) were used to analyze the relationships of soil respiration with soil moisture and temperature in this study. Further, Equation 3 was used to

analyze the combined effect of soil temperature and moisture on soil respiration.

$$R_{(S+L,\ S,\ L)} = a_1 W + b_1 , \tag{1}$$

$$R_{(S+L,\ S,\ L)} = a_2 e^{b_2 T} , \tag{2}$$

$$R_{(S+L,\ S,\ L)} = a_3 T + b_3 W + c , \tag{3}$$

where, $R_{(S+L,\ S,\ L)}$ indicates each kind of soil respiration, e.g., R_{S+L}, R_S, and R_L (μmol/(m^2•s)); W is the soil moisture (%); T is the soil temperature (°C); a_1, b_1, a_2, b_2, a_3, and b_3 are the regression coefficients; and c is the regression constant.

The data were processed and analyzed using Microsoft Excel (Redmond, WA, USA) and SPSS 24.0 (IBM Inc., NY, USA). A one-way analysis of variance (ANOVA) was used to compare the differences in soil respiration and soil parameters among different treatments. A least significant difference (LSD) was performed to assess the differences at the significance level of 0.05. In addition, a two-way ANOVA was applied to analyze the effects of changes in precipitation, N addition, and their interaction on soil respiration and soil parameters. Origin 2023 (OriginLab, Northampton, MA, USA) was used for fitting, correlation analysis, and graphing. We constructed a structural equation model (SEM) using AMOS 24.0 (IBM Inc., NY, USA) based on the maximum likelihood estimation to reveal the key factors influencing the rates of R_{S+L}, R_S, and R_L. Five goodness-of-fit indices were used to evaluate the SEM, namely the cardinality freedom ratio (χ^2/df), root mean square error of approximation (RMSEA), goodness-of-fit index (GFI), adjusted goodness-of-fit index (AGFI), and P-value (P). The model with the index ranges of $\chi^2/df<3$, RMSEA<0.05, GFI>0.9, AGFI>0.9, and $P>0.05$ indicates that the SEM performs well.

3 Results

3.1 Characteristics of the variations in soil parameters

Soil moisture and temperature in the 0–5 cm soil layer showed obvious diurnal and seasonal dynamics under different treatments (Fig. S1). In addition, soil temperature exhibited an obvious single peaked curve compared with soil moisture. N addition significantly increased soil moisture by 14.2% ($P<0.05$). However, there was no significant effect of N addition on soil temperature ($P>0.05$; Fig. 1a). Both the increase and decrease in precipitation significantly affected soil temperature and moisture ($P<0.001$; Fig. 1a).

N addition significantly reduced SMBN by 27.7% ($P<0.05$). In contrast, there was no significant effect of N addition on SMBC (Fig. 1b). Both the increase and decrease in precipitation increased SMBN and SMBC ($P>0.05$; Fig. 1b). N addition increased the contents of TN and SOC by 12.0% ($P<0.05$) and 6.8% ($P>0.05$), respectively (Fig. 1c). Moreover, the decrease in precipitation significantly increased the contents of TN and SOC by 17.8% ($P<0.001$) and 26.3% ($P<0.001$), respectively, while the increase in precipitation did not significantly affect the contents of TN and SOC ($P>0.05$; Fig. 1c). N addition markedly increased the content of soil actinomyces by 20.2% ($P<0.05$), while there were no significant effects of N addition on the contents of soil bacteria, fungi, and protozoa ($P>0.05$; Fig. 1d). The increase in precipitation markedly reduced the contents of soil actinomyces and protozoa by 16.4% ($P<0.001$) and 9.6% ($P<0.001$), respectively, while the decrease in precipitation significantly increased the contents of soil actinomyces and protozoa by 16.8% ($P<0.001$) and 31.3% ($P<0.001$), respectively (Fig. 1d). However, there were no significant effects of the increase and decrease in precipitation on the contents of soil bacteria and fungi ($P>0.05$; Fig. 1d). Changes in precipitation and N addition showed significant interactive effects on soil temperature, SMBN, soil bacteria, and soil actinomyces ($P<0.05$), while no significant interactive effects were observed on soil moisture, SMBC, TN, SOC, soil fungi, and soil protozoa ($P>0.05$; Table 1).

3.2 Characteristics of the variations in soil respiration and its components

R_{S+L} and R_S exhibited similar diurnal dynamics during the entire experimental period (Figs. 2 and

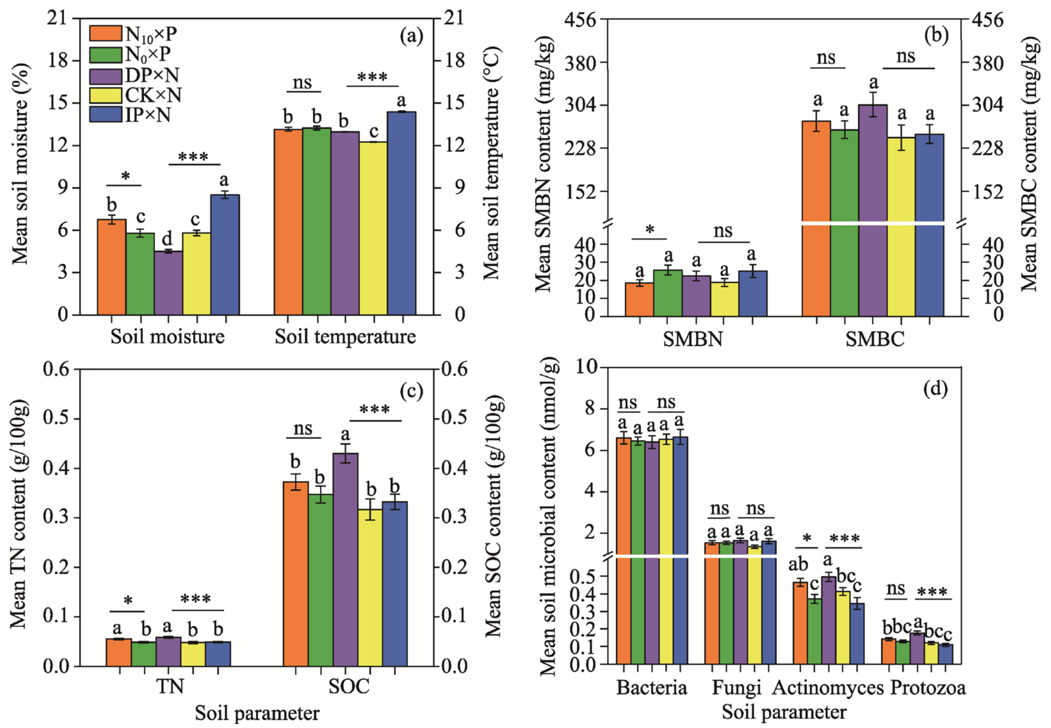

Fig. 1 Variations in mean soil moisture and temperature (a), mean SMBN and SMBC (b), mean TN and SOC (c), and mean soil microbial content (d) under different treatments. SMBN, soil microbial biomass nitrogen; SMBC, soil microbial biomass carbon; TN, total nitrogen; SOC, soil organic carbon. N_0 and N_{10} indicate nitrogen (N) addition rates at 0.0 and 10.0 g/(m^2•a), respectively. CK, IP, and DP represent the precipitation levels of the control, increased precipitation by 30%, and decreased precipitation by 30%, respectively. N_0×P indicates the treatments of CK+N_0, IP+N_0, and DP+N_0; N_{10}×P indicates the treatments of CK+N_{10}, IP+N_{10} and DP+N_{10}; DP×N indicates the treatments of DP+N_0 and DP+N_{10}; CK×N indicates the treatments of CK+N_0 and CK+N_{10}; IP×N indicates the treatments of IP+N_0 and IP+N_{10}. Different lowercase letters indicate significant differences among different treatments for the same soil parameter at P<0.05 level based on the Duncan's test. * indicates significant differences among N addition treatments or among precipitation change treatments at P<0.05 level based on the Duncan's test; *** indicates significant differences among N addition treatments or among precipitation change treatments at P<0.001 level based on the Duncan's test; ns indicates no significant differences among N addition treatments or among precipitation change treatments at P>0.05 level based on the Duncan's test. Bars mean standard errors.

Table 1 Effects of changes in precipitation, nitrogen (N) addition, and their interaction (changes in precipitation×N addition) on soil parameters

Soil parameter	Changes in precipitation		N addition		Changes in precipitation×N addition	
	F	*P*	*F*	*P*	*F*	*P*
Soil moisture	145.451	***	24.343	***	5.716	*
Soil temperature	940.636	***	3.854	ns	1.407	ns
SMBN	1.409	ns	5.212	*	5.839	*
SMBC	2.422	ns	0.420	ns	0.783	ns
TN	10.467	***	10.318	*	1.295	ns
SOC	11.204	***	1.434	ns	2.595	ns
Bacteria	0.171	ns	0.194	ns	3.278	*
Fungi	2.353	ns	0.003	ns	1.188	ns
Actinomyces	9.834	***	11.37	***	9.361	***
Protozoa	14.234	***	1.503	ns	0.237	ns

Note: SMBN, soil microbial biomass nitrogen; SMBC, soil microbial biomass carbon; TN, total nitrogen; SOC, soil organic carbon. *, significance at P<0.05 level; ***, significance at P<0.001 level; ns, not significant.

3). The highest and lowest rates of soil respiration were observed at 12:00–14:00 and 02:00–04:00, respectively. However, the dynamics of R_L were complex, and the maximum and minimum rates of R_L did not appear at the same time in different seasons (Fig. 4). In addition, the seasonal dynamics of the rates of R_{S+L}, R_S, and R_L followed the order of summer>spring>autumn>winter (Fig. S2). The daily average R_{S+L} rate under all treatments ranged from 0.08 (±0.01) to 0.51 (±0.03) μmol/(m^2•s) in different seasons (Fig. 2). In addition, R_{S+L} rate differed significantly among different precipitation change treatments in autumn and winter (P<0.05; Fig. 2f and h). The daily average R_S rate ranged from 0.03 (±0.00) to 0.39 (±0.02) μmol/(m^2•s) (Fig. 3), and there were significant differences among N addition treatments in spring (P<0.05; Fig. 3a), as well as significant differences among different precipitation change treatments in spring, autumn, and winter (P<0.05; Fig. 3b, f, and h). The daily average R_L rate ranged from 0.01 (±0.00) to 0.08 (±0.01) μmol/(m^2•s) in different seasons (Fig. 4). In addition, the results revealed significant differences in the R_L rate among precipitation change treatments in different seasons (P<0.05; Fig. 4b, d, f, and h).

N addition markedly increased the rates of R_{S+L} and R_S by 4.8% and 8.0%, respectively, compared with the treatment without N addition (P<0.05; Fig. 5a). The increase in precipitation increased the rates of R_{S+L} and R_S by 2.3% (P<0.05) and 5.7% (P<0.001), respectively (Fig. 5a). In addition, the decrease in precipitation significantly increased the rates of R_{S+L} and R_S by 12.9% (P<0.05) and 23.4% (P<0.001), respectively (Fig. 5a). We also observed a lack of significant effects of precipitation change and N addition treatments on the R_L rate (Fig. 5a). R_L/R_{S+L} under different treatments ranged from 24.85% (±2.56%) to 30.07% (±2.92%) (Fig. 5b). Furthermore, we identified significant interactive effect of changes in precipitation and N addition on the rates of R_{S+L}, R_S, and R_L (P<0.001; Table 2).

3.3 Relationships between soil respiration and soil parameters

Figure 6 indicated the relationships of soil respiration (R_{S+L}, R_S, and R_L) with soil temperature and moisture. The rates of R_{S+L}, R_S, and R_L showed significant and positive exponential relationships with soil temperature, with R^2 values of 0.60 (P<0.001), 0.45 (P<0.001), and 0.37 (P<0.001), respectively (Fig. 6a, c and e). In addition, the rates of R_{S+L}, R_S, and R_L exhibited significant linear relationships with soil moisture (P<0.05; Fig. 6b, d and f). The rates of R_{S+L}, R_S, and R_L also exhibited significant linear relationships with the interaction of soil temperature and moisture (P<0.001; Table S2). The results demonstrated that soil temperature was the primary abiotic factor that affected the changes in the rates of R_{S+L}, R_S, and R_L, compared with soil moisture.

The correlation analysis showed significant positive correlations of R_{S+L} rate with TN (P<0.05), SOC (P<0.001), and SMBC (P<0.01) (Fig. 7). R_S rate significantly and positively correlated with TN (P<0.01), SOC (P<0.001), SMBC (P<0.05), soil actinomyces (P<0.05), and soil protozoa (P<0.01) (Fig. 7). However, R_L rate only positively correlated with SOC (P<0.05) and SMBC (P<0.05) (Fig. 7).

According to the results of SEM, changes in precipitation and N addition exhibited positive effects on the soil hydrothermal factors (soil temperature and moisture) and negative effects on the soil C (SOC and SMBC) and microorganisms (actinomyces and protozoa). Soil C positively affected R_{S+L} rate, while soil hydrothermal factors, C, and microorganisms positively affected R_S rate. Changes in precipitation, N addition, and soil C positively affected R_L rate. It is apparent that SMBC and SOC were the key factors that controlled R_{S+L} (Beta=0.59; Fig. 8a1 and a2), R_S (Beta=0.39; Fig. 8b1 and b2), and R_L (Beta=0.37; Fig. 8c1 and c2).

4 Discussion

4.1 Effects of changes in precipitation and N addition on soil parameters

Arid and semi-arid desert steppes are typical ecosystems with limited water resources and soil nutrients (Hooper and Johnson, 1999; Yan et al., 2011). The soil microenvironments, particularly

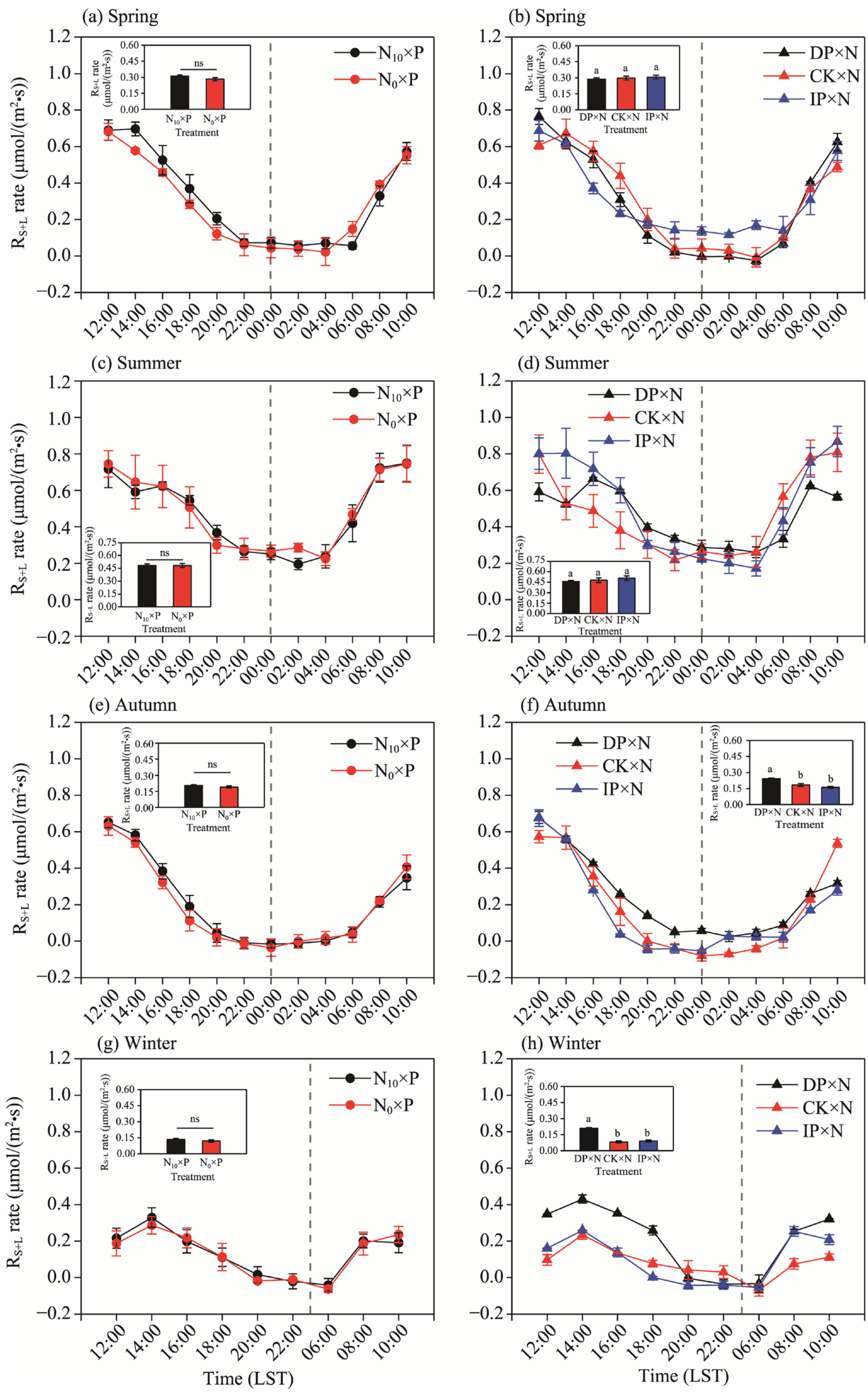

Fig. 2 Diurnal dynamics in soil respiration with litter (R_{S+L}) in spring (a and b), summer (c and d), autumn (e and f), and winter (g and h) under different treatments. Small figures show the daily average R_{S+L} rate under different treatments. Different lowercase letters indicate significant differences among precipitation change treatments at $P<0.05$ level based on the Duncan's test; ns indicates no significant differences among N addition treatments at $P>0.05$ level based on the Duncan's test. Bars mean standard errors.

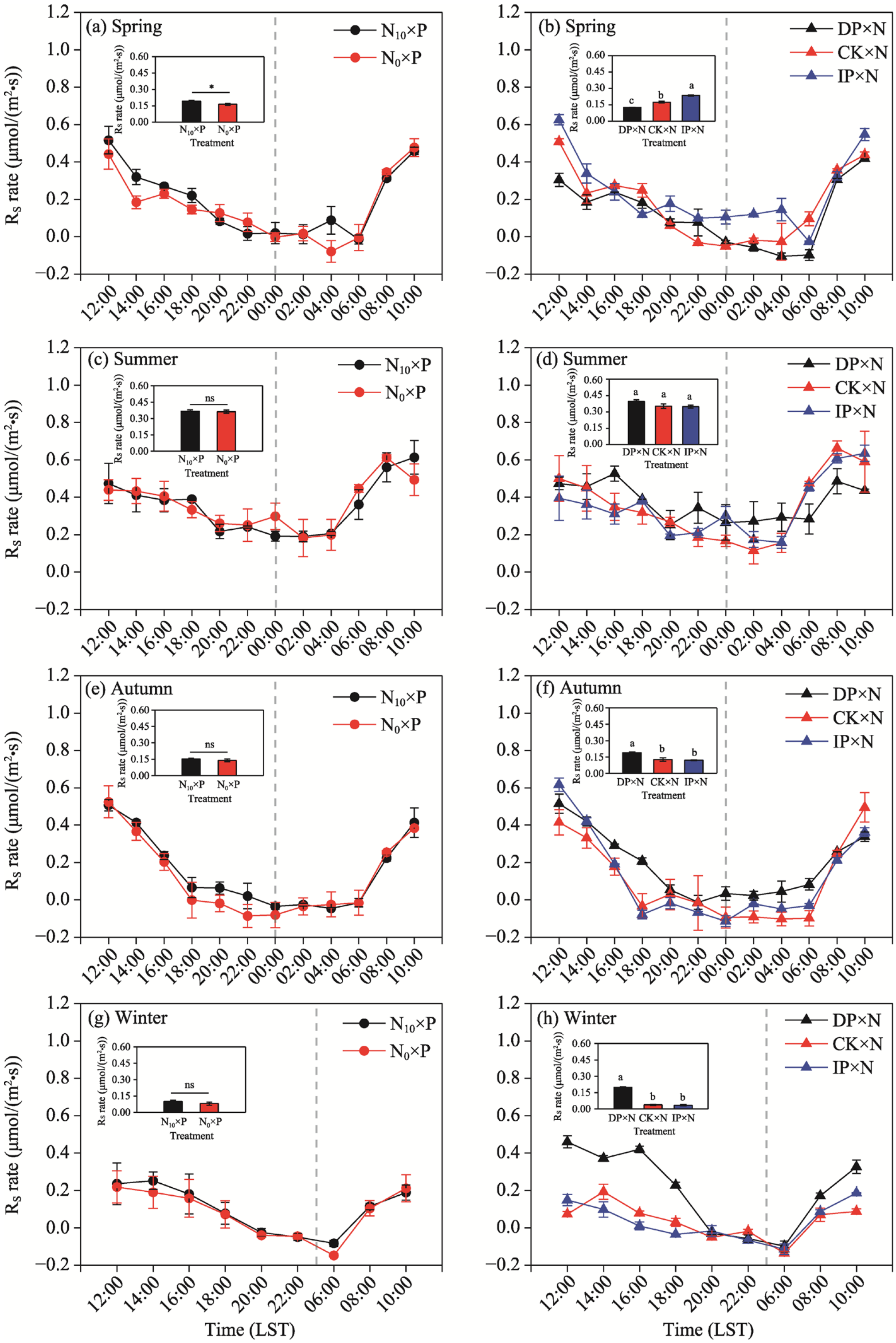

Fig. 3 Diurnal dynamics in soil respiration without litter (Rs) in spring (a and b), summer (c and d), autumn (e and f), and winter (g and h) under different treatments. Small figures show the daily average Rs rate under different treatments. Different lowercase letters indicate significant differences among precipitation change treatments at $P<0.05$ level based on the Duncan's test; * indicates significant differences among N addition treatments at $P<0.05$ level based on the Duncan's test; ns indicates no significant differences among N addition treatments at $P>0.05$ level based on the Duncan's test. Bars mean standard errors.

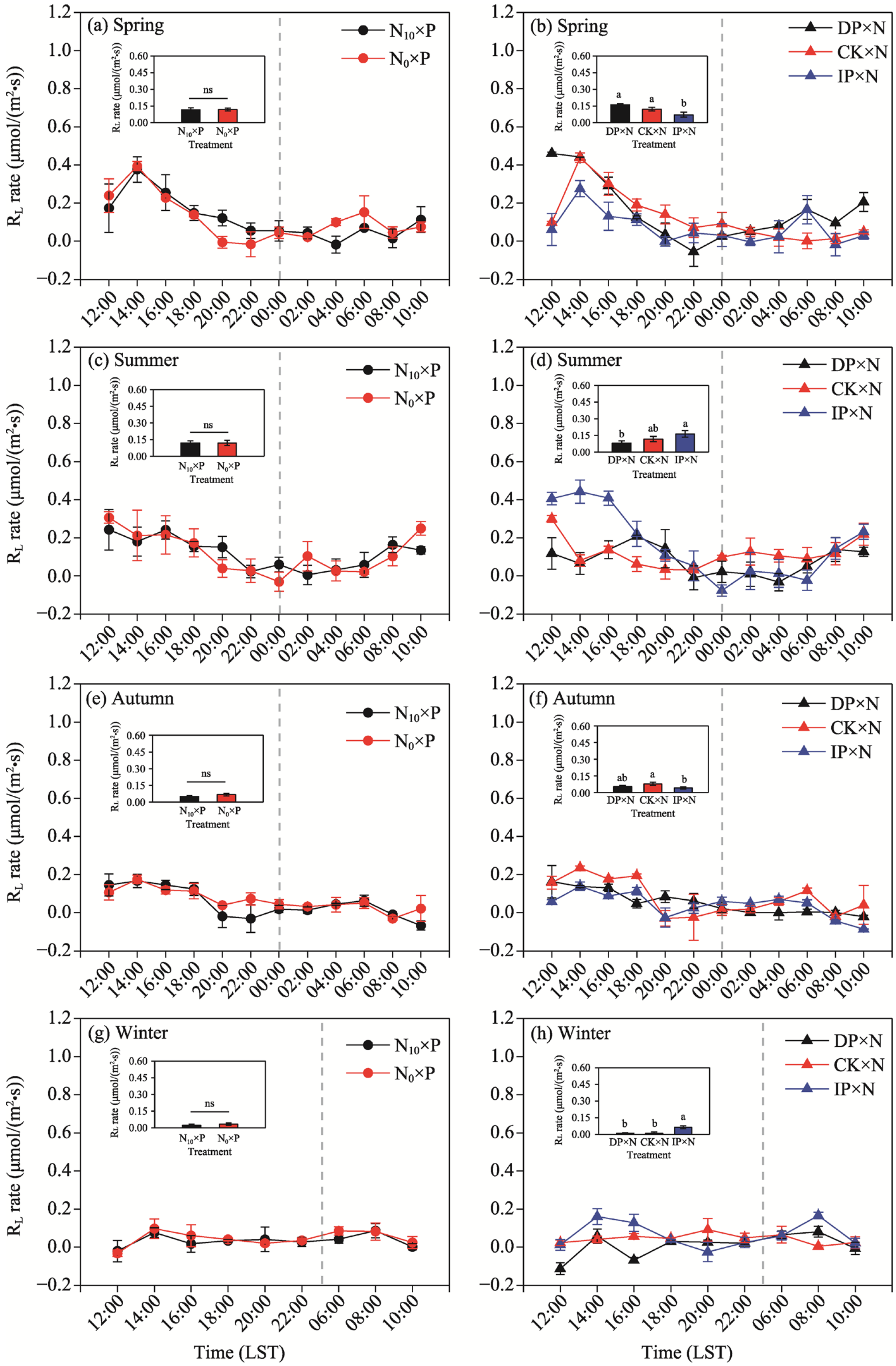

Fig. 4 Diurnal dynamics in litter respiration (R_L) in spring (a and b), summer (c and d), autumn (e and f), and winter (g and h) under different treatments. Small figures show the daily average R_L rate under different treatments. Different lowercase letters indicate significant differences among precipitation change treatments at $P<0.05$ level based on the Duncan's test; ns indicates no significant differences among N addition treatments at $P>0.05$ level based on the Duncan's test. Bars mean standard errors.

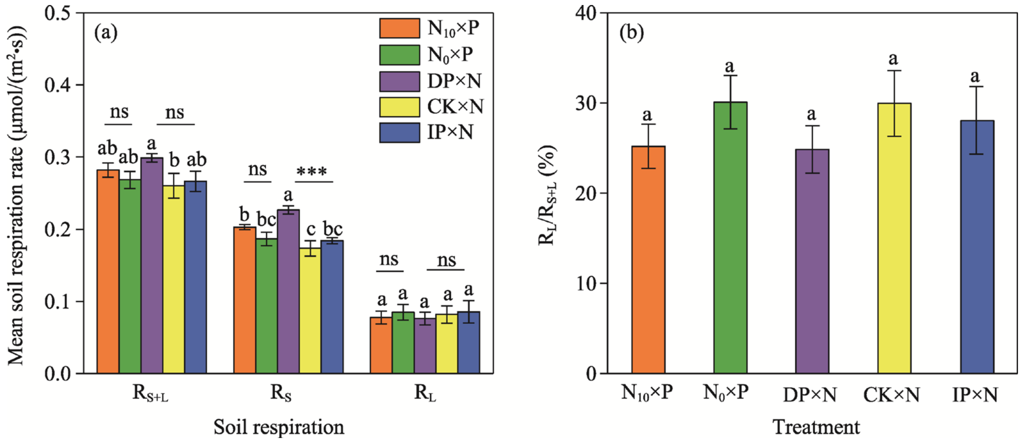

Fig. 5 Mean soil respiration (R_{S+L}, R_S, R_L) rate (a) and litter respiration contribution (R_L/R_{S+L}) (b) under different treatments. Different lowercase letters indicate significant differences among different precipitation change and N addition treatments at $P<0.05$ level based on the Duncan's test. *** indicates significant differences among N addition treatments or among precipitation change treatments at $P<0.001$ level based on the Duncan's test; ns indicates no significant differences among N addition treatments or among precipitation change treatments at $P>0.05$ level based on the Duncan's test. Bars mean standard errors.

Table 2 Effects of changes in precipitation, N addition, and their interaction on soil respiration with litter (R_{S+L}), soil respiration without litter (R_S), and litter respiration (R_L)

Factor	R_{S+L}		R_S		R_L	
	F	*P*	*F*	*P*	*F*	*P*
Changes in precipitation	4.452	*	59.160	***	0.203	ns
N addition	1.437	ns	14.994	***	0.358	ns
Changes in precipitation×N addition	28.065	***	101.511	***	13.733	***

Note: *, significance at $P<0.05$ level; ***, significance at $P<0.001$ level; ns, not significant.

soil temperature and moisture, have extremely sensitive responses to climate change. In this study, we found similar patterns of diurnal and seasonal soil temperature and moisture under different treatments (Fig. S1), which are consistent with the findings of previous related studies (Cui and Zhang, 2016; Zhao et al., 2020). We hypothesized that soil temperature and moisture varied largely with the atmospheric temperature and precipitation. However, N addition can enhance the contact of litter with soil (Li et al., 2016) and prevent the losses of soil moisture, which explains the significant effects of N addition on the average value of soil moisture in this study (Fig. 1a). In addition, changes in precipitation exhibited significant influences on the average values of soil temperature and moisture (Fig. 1a), which are consistent with the findings in previous studies on the characteristics of soil temperature and moisture in grasslands (Zhao et al., 2014; Zhao et al., 2020).

Many studies have highlighted the importance of soil nutrients and microbial community in assessing soil fertility (Sun et al., 2014; Gao et al., 2018). Xiao et al. (2020) demonstrated the key role of N addition in promoting soil microbial activity and enhancing the efficiency of soil microorganism at utilizing nutrients, which is consistent with the results of this study. These findings demonstrated the significant effects of N addition on the increase of SMBC, TN, SOC, and soil microbial community (Fig. 1b–d). The reason might be that N addition promoted the decomposition of litter and accelerated the flow of nutrients in the soil (Miao et al., 2020; Wilcots et al., 2022), which was demonstrated by the significant positive correlations among soil microorganisms, temperature, moisture, TN, SOC, SMBN, and SMBC in this study ($P<0.05$; Fig. 7). In addition, owing to the limited leaching of soil nutrients under low precipitation, the decrease in precipitation increased the contents of soil nutrients and microbial biomass, compared

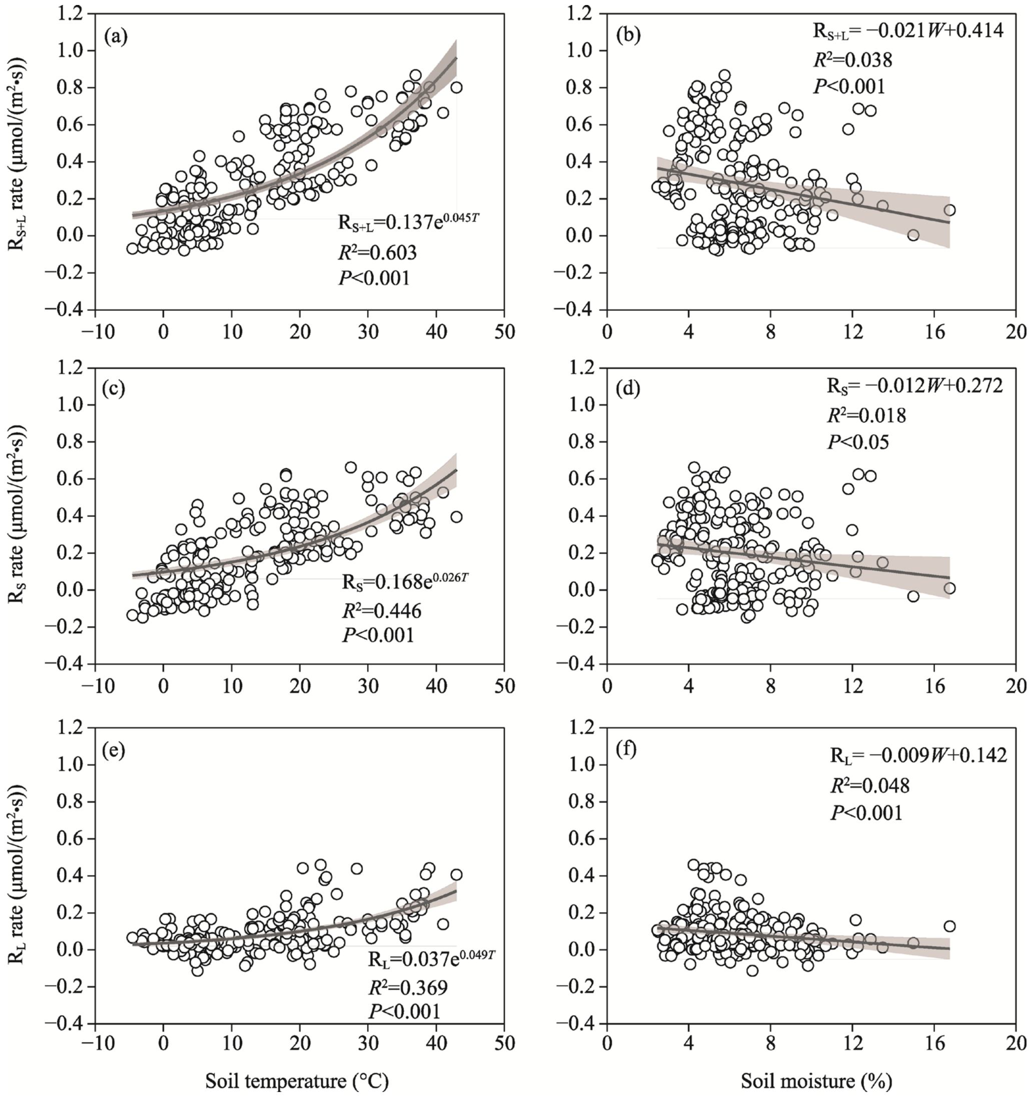

Fig. 6 Relationships of soil respiration (R_{S+L}, R_S, and R_L) with soil temperature (a, c, and e) and soil moisture (b, d, and f). T, soil temperature; W, soil moisture. The shaded part represents a 95% confidence interval.

with normal and increased precipitation (Fig. 1b–d), thereby accumulating soil nutrients in the upper soil layer. Similar findings were reported by Fang et al. (2017) and Zhao et al. (2020). However, some studies highlighted the impact of low precipitation in reducing the infiltration rate of soil moisture and thus decreasing the utilization rate of organic matter by soil microorganisms, which may consequently lead to a reduction in the contents of soil microbial biomass (Li et al., 2020; Ondier et al., 2020).

4.2 Effects of changes in precipitation and N addition on soil respiration

The obvious diurnal and seasonal variations in soil respiration rates demonstrated that the desert steppe ecosystem is highly vulnerable to environmental changes (Gao et al., 2018; Tiruvaimozhi and Sankaran, 2019; Wang et al., 2020). In addition, changes in precipitation and N addition caused similar diurnal and seasonal dynamics of soil respiration rates (Figs. 2–4 and S2), which suggested that the dynamics in soil respiration might be related to other factors (Wang et al., 2013; Li et al., 2021). We also found that the dynamics of the rates of R_{S+L} and R_S were very similar to that of soil temperature, indicating that soil temperature is closely related to soil respiration (Ondier et al., 2020).

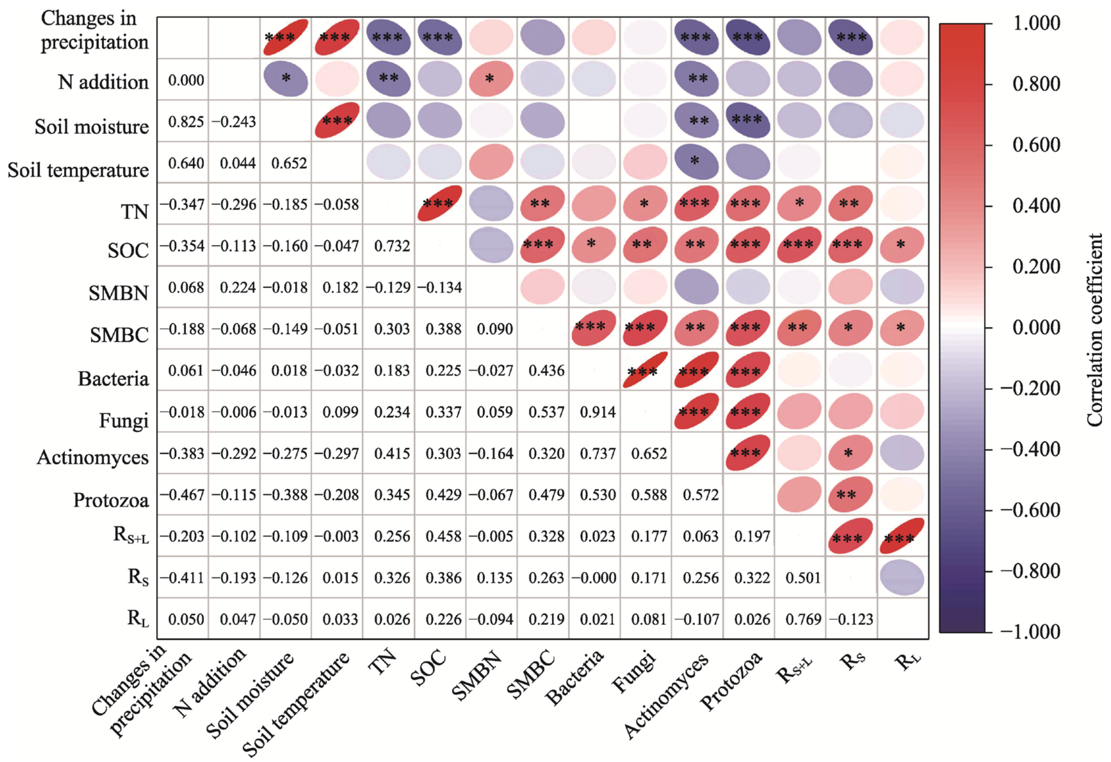

Fig. 7 Correlation coefficients among soil respiration (R_{S+L}, R_S, and R_L), biotic factors (soil microorganisms) and abiotic factors (soil temperature, moisture, TN, SOC, SMBN, and SMBC, as well as changes in precipitation and N addition). *, significance at $P<0.05$ level; **, significance at $P<0.01$ level; ***, significance at $P<0.001$ level. Ellipses of different shapes indicate different significant sizes.

The enhancement of soil respiration caused by N addition may be due to the increase in available N content, which can promote soil microbial activity and productivity (Hasselquist et al., 2012; Deng et al., 2018; Wang et al., 2019b). Other studies have suggested that N addition may increase soil N content, thereby weakening the utilization rates of N by soil microorganisms and reducing soil respiration to some extent (Janssen et al., 2010; Sun et al., 2014). This study revealed that N addition significantly increased the rates of R_{S+L} and R_S by 4.8% and 8.0%, respectively ($P<0.05$; Fig. 5a). However, N addition decreased the R_L rate by 8.6% ($P>0.05$; Fig. 5a), which is consistent with the findings in previous studies of Schlesinger and Andrews (2000) and Lee and Jose (2003). Han et al. (2019) highlighted the role of N addition in promoting the decomposition of litter and enhancing the efficiency of utilizing soil nutrients, thereby increasing soil microbial respiration. In addition, our results showed a greater increase in R_S rate than in R_{S+L} rate under N addition treatment, which may be caused by a decrease in R_L rate (Fig. 5a). This might be due to the utilization of soil nutrients by soil microorganisms to synthesize their compounds, which promoted the sequestration of soil C. Moreover, this can also be attributed to the presence of Gramineae (such as *Agropyron mongolicum* and *Stipa breviflora*) and Leguminosae (such as *Sophora alopecuroides*) in plant litter, which decreased the sensitivity of soil respiration to N compared with that in other plant communities (Xu et al., 2015). However, other studies have shown that the effects of N addition are often dependent on soil moisture, demonstrating the critical role of changes in precipitation in weakening the effects of N addition on soil respiration (Hooper and Johnson, 1999; Li et al., 2011).

Changes in precipitation can affect soil respiration by altering SMBC, soil temperature, moisture, and total C (Zhou et al., 2016; Deng et al., 2017). However, the factors that influence soil respiration vary in different ecosystems (Zhang et al., 2019b). In this study, we removed the living plants and roots from the surface soil of treatment plots to ensure that the soil nutrients

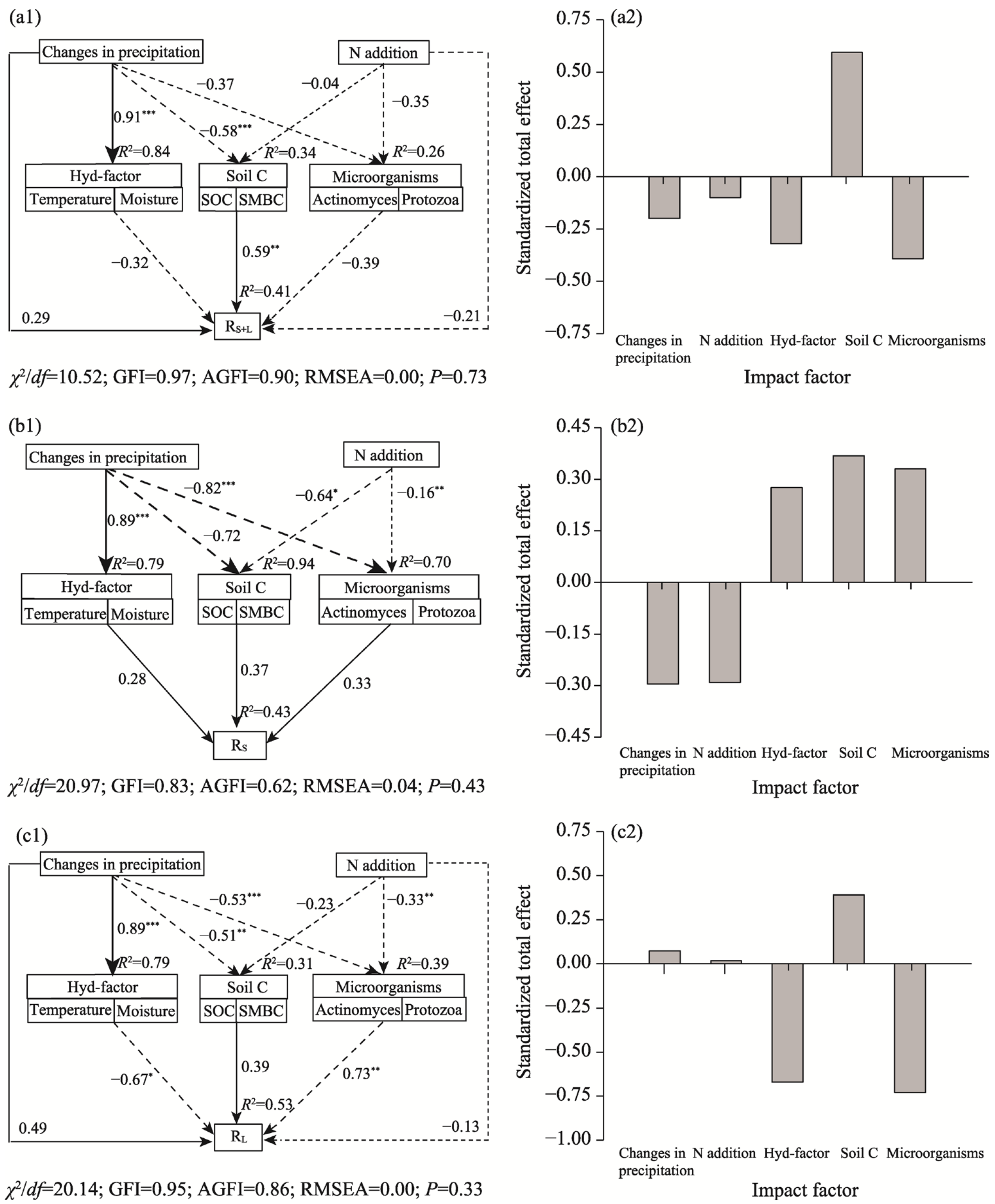

Fig. 8 Results of the structural equation model (SEM) reflecting the multivariate effects of biotic factors (soil microorganisms) and abiotic factors (soil temperature, moisture, SOC, and SMBC, as well as changes in precipitation and N addition) on R_{S+L} (a1 and a2), R_S (b1 and b2), and R_L (c1 and c2). Hyd-factor, soil hydrothermal factors; Soil C, soil carbon; χ^2/df, cardinality freedom ratio; GFI, goodness-of-fit index; AGFI, adjusted goodness-of-fit index; RMSEA, root mean square error of approximation. Arrows show the effects of different factors on soil respiration. Values around the solid and dashed lines indicate positive and negative effects, respectively. The thickness of the line reflects the absolute value size of the correlation coefficient, for example, the thicker the line, the stronger the correlation. *, significance at P<0.05 level; **, significance at P<0.01 level; ***, significance at P<0.001 level.

needed by microorganisms were primarily originated from the litter. The increase in precipitation increased the rates of R_{S+L} and R_S by 2.3% and 5.7%, respectively (Fig. 5a), but the magnitude of the increase observed in treatment plots without litter was higher than that in treatment plots with litter, which is consistent with the results reported by Liu et al. (2016) and Song et al. (2019).

Zhou et al. (2019) highlighted the substantial effects of increased precipitation in enhancing the utilization efficiency of soil C and stimulating soil respiration. The low magnitude of the increase in R_{S+L} rate might be due to the immobilization of C that soil microorganisms derive from litter. Many previous studies have found that low precipitation can result in limited soil moisture, which restrains the distribution of belowground C and the supply of C substrates in the soil (Peng et al., 2020; Yang et al., 2022b), thereby inhibiting soil enzymes, microbial activities, and microbial respiration (Or et al., 2007; Suseela and Dukes, 2013). In this study, the decrease in precipitation increased the rates of R_{S+L} and R_S by 12.9% and 23.4%, respectively (Fig. 5a), indicating a higher magnitude of increase in the rates of R_{S+L} and R_S than those observed under increased precipitation treatment. Previous studies have demonstrated that low precipitation can reduce the accumulation of soil moisture and the leaching of soil nutrients (Liu et al., 2009; Zhang et al., 2019c; Zhang et al., 2021). These findings demonstrated the substantial effects of the decrease in precipitation on increasing soil nutrients and the contents of soil microorganisms (Fig. 1b–d). In addition, in arid and semi-arid desert steppes, intense precipitation events primarily occur during the growing season, which can enhance soil compaction and limit soil aeration (Knapp et al., 2008). Grote et al. (2010) demonstrated the significant effects of increased precipitation in limiting the rates of oxygen transport with water in arid ecosystems, thereby inhibiting soil respiration. These are consistent with the findings of this study, which showed reductions in the contents of soil actinomycetes and protozoa under increased precipitation treatment (Fig. 1d).

4.3 Correlations between soil respiration and soil parameters under precipitation change and N addition treatments

Ondier et al. (2020) found that soil respiration is closely related to the surface soil temperature. In this study, soil temperature exhibited a significant exponential relationship with soil respiration, compared with soil moisture (Fig. 6a, c and e), which is inconsistent with the results reported by Yu et al. (2022). These findings highlighted soil temperature as the key factor in affecting changes in soil respiration in arid and semi-arid ecosystems. This result might be owing to the decrease in surface soil moisture as a result of the drastic change in precipitation, thus lessening the effects of soil moisture on respiration (Deng et al., 2017). In addition, the large differences in diurnal soil temperature in desert steppes can lead to a decrease in surface soil moisture independently of soil respiration (Wang et al., 2019a). In contrast, a suitable soil temperature can promote the activity of soil enzymes and microorganisms (Feng et al., 2018), which may enhance the utilization efficiency of soil C and subsequently affect soil respiration. The results of this study showed that changes in precipitation significantly and positively correlated with soil temperature and moisture (P<0.001; Fig. 7), which are consistent with the results of SEM (P<0.001; Fig. 8a–c). In addition, the results of SEM demonstrated the positive effects of soil temperature and moisture on R_S rate (Fig. 8b), indicating that the removal of litter would reduce the inputs of soil nutrients (Chen et al., 2012). This might be due to the antagonistic action of different factors that soil respiration increased with increasing soil temperature but negatively correlated with soil moisture (Fig. 6c and d). However, the results of SEM also indicated that hydrothermal factors have a positive effect on R_S rate (Fig. 8b).

Numerous studies have found that the response of soil respiration to climate change is the result of the combined effect of soil parameters, namely antagonistic and synergistic effects (Liu et al., 2009; Zhang et al., 2019; Miao et al., 2020). Our results showed that SOC and SMBC are the key factors affecting the rates of R_{S+L}, R_S, and R_L (Fig. 8a and b). In addition, several field control experiments highlighted the fact that soil microorganisms are the primary indicators that can reflect the influences of litter on soil respiration (Muraskiene et al., 2020), due to the ability of soil microorganisms to fix C from litter (Sui and Zhou, 2013; Xun et al., 2016). This ability could explain the positive effects of soil microorganisms on R_S rate and the negative effects on the rates of R_{S+L} and R_L (Fig. 8). In addition, SOC and SMBC are easily mineralized and utilized by soil microorganisms, resulting in the release of CO_2 (Zhou et al., 2016; Deng et al., 2017). Results of correlation analysis indicated a positive correlation between soil microorganisms and

nutrients (Fig. 7). In this study, the mean R_L/R_{S+L} value was 27.63% (Fig. 5b), which is consistent with the results reported by Boone et al. (1998) and Zhao et al. (2020). This finding is mainly due to the fact that litter decomposition increases soil nutrients and provides a substrate for soil heterotrophic respiration (Zhao et al., 2020). Litter is the primary source of C for soil respiration in the surface soil layer. Indeed, a portion of C can be decomposed by soil microorganisms, leading to the release of CO_2, and the remaining portion of C can be immobilized by soil microorganisms to form soil organic matter (Ngao et al., 2005). The results of SEM showed positive effects of changes in precipitation and N addition on R_L rate (Fig. 8c), which can be explained by the key roles of changes in precipitation and N addition in promoting litter decomposition that leads to the loss of C from litter in the soil (Chimney and Pietro, 2006).

5 Conclusions

In this study, the characteristics of variations in soil respiration and its components (R_{S+L}, R_S, and R_L) in a desert steppe in Yanchi County were assessed under short-term changes in precipitation and N addition treatments, and the primary factors that affect soil respiration in the context of climate change were delineated. The results demonstrated significant effects of N addition, as well as increased and decreased precipitation, in promoting the rates of R_{S+L} and R_S. In contrast, there were no significant effects of changes in precipitation and N addition on R_L rate. In addition, the mean R_L/R_{S+L} value observed under different treatments was 27.63%, indicating that R_L is one of the most important components of soil respiration in desert steppe ecosystems. Furthermore, soil microorganisms, soil temperature, soil moisture, TN, and SOC were the primary factors that controlled soil respiration in the desert steppe. Of these factors, soil temperature, SOC, and SMBC were the most important. Litter decomposition is a long-term process; thus, it is necessary to continue to explore the responses of soil respiration to climate change through long-term monitoring to provide more evidence for the C emissions in desert steppe ecosystems.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Conceptualization: MA Jinpeng, PANG Danbo, CHEN Lin; Methodology: MA Jinpeng, LI Xuebin; Formal analysis: MA Jinpeng, LI Xuebin; Writing - review and editing: MA Jinpeng; Supervision: PANG Danbo, CHEN Lin; Software: HE Wenqiang, ZHANG Yaqi, WU Mengyao; Funding acquisition: LI Xuebin.

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Appendix

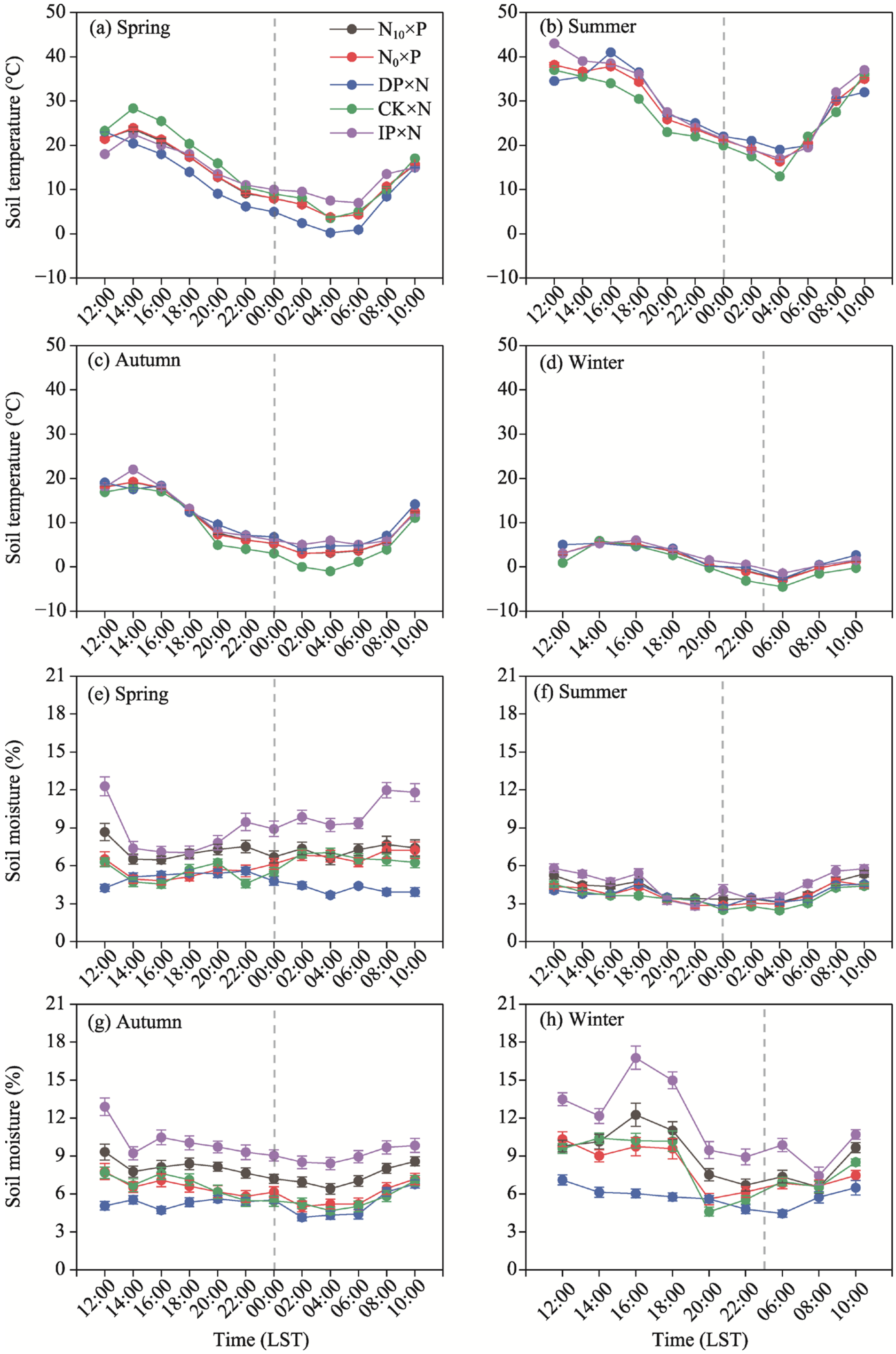

Fig. S1 Diurnal dynamics of soil temperature and moisture in spring (a and e), summer (b and f), autumn (c and g), and winter (d and h) under different treatments. N_0 and N_{10} indicate nitrogen (N) addition rates at 0.0 and 10.0 g/(m^2•a), respectively. CK, IP, and DP indicate the precipitation levels of the control, increased precipitation by 30%, and decreased precipitation by 30%, respectively. N_0×P indicates the treatments of CK+N_0, IP+N_0, and DP+N_0; N_{10}×P indicates the treatments of CK+N_{10}, IP+N_{10}, and DP+N_{10}; DP×N indicates the treatments of DP+N_0 and DP+N_{10}; CK×N indicates the treatments of CK+N_0 and CK+N_{10}; IP×N indicates the treatments of IP+N_0 and IP+N_{10}. Bars mean standard errors.

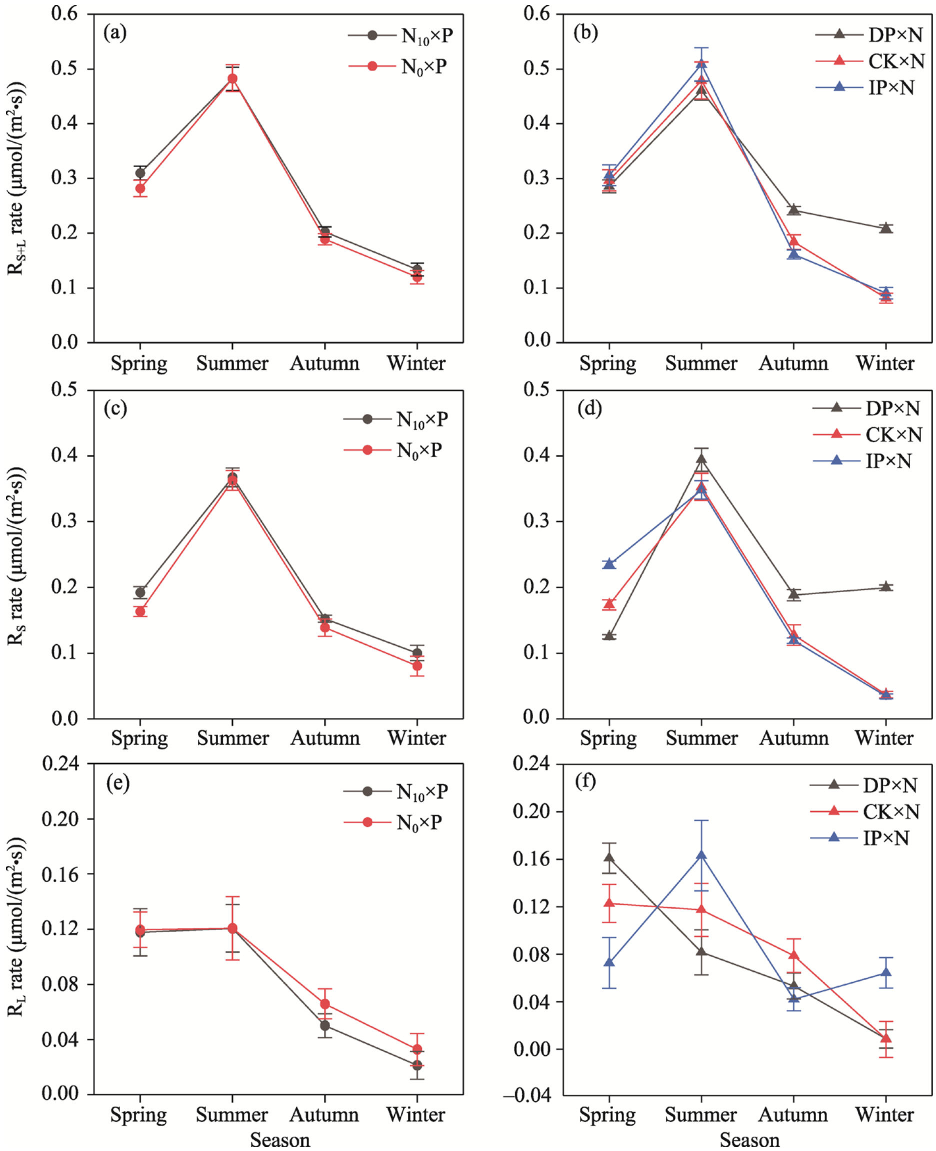

Fig. S2 Seasonal dynamics in (a and b) soil respiration with litter (R_{S+L}), (c and d) soil respiration without litter (R_S), and (e and f) litter respiration (R_L) under different treatments. Bars mean standard errors.

Table S1 Characteristics of litter indices of the four typical plant species in the study area

Index	*Stipa breviflora*	*Sophora alopecuroides*	*Agropyron mongolicum*	*Artemisia scoparia*	*F*	*P*
Cellulose content (g/100 g)	14.14±0.10^{d}	10.08±0.20^{c}	15.44±0.08^{b}	16.18±0.14^{a}	394.9	***
Hemicellulose content (g/100 g)	18.23±0.39^{a}	11.48±0.15^{d}	14.98±0.20^{b}	12.57±0.16^{c}	148.0	***
Lignin content (g/100 g)	28.65±0.05^{b}	28.37±0.15^{b}	29.17±0.20^{a}	28.34±0.16^{b}	6.6	*
TN content (g/100 g)	1.53±0.02^{c}	3.28±0.04^{a}	1.75±0.09^{b}	1.35±0.04^{d}	256.5	***
TP content (g/100 g)	0.05±0.00^{c}	0.17±0.02^{a}	0.08±0.01^{bc}	0.11±0.01^{b}	22.3	***
TC content (g/100 g)	35.81±1.17^{c}	42.70±0.49^{b}	42.38±0.70^{b}	50.74±1.24^{a}	41.0	***

Note: TN, total nitrogen; TP, total phosphorus; TC, total carbon. Different lowercase letters indicate significant differences among different litter indices at $P<0.05$ level based on the Duncan's test. *, significance at $P<0.05$ level; ***, significance at $P<0.001$ level. Mean±SE.

Table S2 Composite functional parameters of soil respiration with litter (R_{S+L}), soil respiration without litter (R_S), and litter respiration (R_L) with soil temperature and moisture

Soil respiration	Equation	*a*	*b*	c	*P*	R^2
R_{S+L}	$R_{S+L}=0.020T+0.019W-0.107$	0.020	0.019	–0.107	***	70.990
R_S	$R_S=0.014T+0.016W-0.010$	0.014	0.016	–0.010	***	57.090
R_L	$R_L=0.005T+0.003W-0.007$	0.005	0.003	–0.007	***	33.902

Note: T, soil temperature; W, soil moisture. a and b are the regression coefficients, and c is the regression constant. ***, significance at $P<0.001$ level.